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Polypodium appalachianum: An Unusual Tree Canopy Epiphyte in the Great Smoky Mountains National Park

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ABSTRACT.—The typically lithophilic *Polypodium appalachianum* was discovered as a canopy epiphyte 35 to 40 m above ground on a horizontal branch of a champion-size *Liriodendron tulipifera* in the Great Smoky Mountains National Park. Occurring along with this first documentation of *P. appalachianum* from the tree canopy was an assemblage of normally terrestrial mosses, an unusual assortment of collembola (springtails), and a flightless proturan insect species previously known only from soil and litter. The distinctive features of this canopy habitat may duplicate some ecological conditions usually found only at ground level, establishing the opportunity for translocating an entire community and providing biologists with new insights on the origin of some epiphytes.

Species of *Polypodium* in North America grow on rocky surfaces, soil, rotted wood on ground sites, and as epiphytes on living trees (Tryon and Tryon, 1982). As currently circumscribed, there are approximately 100 species worldwide (Haufler *et al.*, 1993). *Polypodium appalachianum* Haufler and Windham, often called the "Rock Cap" fern because it usually festoons the crowns of large boulders, is one of three *Polypodium* species native to eastern North America. *Polypodium appalachianum* has been reported from the eastern Tennessee counties of Blount, Sevier, and Cocke and in the western North Carolina counties of Hayward and Swain, all within the boundaries of the Great Smoky Mountains National Park (GSMNP). Although occasionally epiphytic at the base of tree trunks (Patricia Cox, pers. comm.), discovery of *P. appalachianum* growing high in the canopy of a champion-sized, living *Liriodendron tulipifera* L. (Yellow Tulip Poplar) tree in the GSMNP represents an epiphytic microhabitat not previously documented. In this paper, we describe the canopy microhabitat of *P. appalachianum* and associated mosses, compare the vertical distribution of bryophytes along the main trunk axis with the horizontal branch that supported the fern microhabitat, briefly describe the climbing techniques used to access the tree canopy, and provide a description and photographs of specimens collected from the tree canopy.

Study Area and Sampling Methods

The GSMNP comprises more than 200,000 ha and serves as a refuge for one of the richest and most diverse biotas in the temperate regions of the world. It also has the largest remaining tracts of old growth forest in eastern United States, estimated at 40,000 ha. As part of a research effort to inventory all of the life forms in the park, the All Taxa Biodiversity Inventory (ATBI) established 20 one-hectare study plots located in major habitats throughout the park. Site selection was based on major forest/vegetation types, elevation and relative accessibility. Two giant *Liriodendron tulipifera* trees are located 1,021 m above sea level on each side of the Ramsay Cascades Trail approximately 1.61 km from the trailhead in the Tennessee part of the park. This is near but outside the ATBI Ramsay Cascades study site and within the Cove Hardwood-Eastern Hemlock forest type found throughout the Ramsay Prong ravine. These trees were called "majestic Roman columns" by Gove (1994) along with a description of the Ramsay Cascades Trail in a popular hiking trail book. *Polypodium appalachianum* was collected August 2, 2001, from the canopy of one of the giant *Liriodendron tulipifera* trees (#307), which measured 169 cm in diameter at breast height and 52.8 m in total height.

During the summers of 2000 and 2001 Central Missouri State University students participating in a tree canopy biodiversity study in the GSMNP climbed and collected bark and epiphyte samples from a total of 240 trees representing 35 different species. The climbers used the double rope climbing technique to access the tree canopy. This technique allows the climber to advance from branch to branch in order to reach higher levels of the tree canopy (Counts *et al.*, 2000). Specimens of epiphytes along with bark samples were collected at approximately 3 m increments. Height above ground was measured by an elevation line attached to the climber's harness.

Results

The *Liriodendron tulipifera* sampled and others in the vicinity were covered with epiphytic mosses and liverworts near the trunk bases. Ferns were absent from the vertical trunks. In the eastern United States little is known about the occurrence of bryophytes in tree canopies and we know of no publications reporting canopy occurrences for any of the species reported here. Table 1 lists the bryophytes identified from bark samples collected at several heights above ground on tree #307. The most remarkable species above 30.5 m are the mosses *Rhodobryum roseum*, *Trichostomum tenuirostre*, and the liverwort *Jamesoniella autumnalis* because these species are usually restricted to the extreme bases of trees. We have seen *J. autumnalis* as a rarity at 2 m above the ground on vertical tree trunks but never *R. roseum* or *T. tenuirostre*, the latter being more commonly found on rock (Crum and Anderson, 1981). The assemblage of species reported in Table 1 is typical of lower tree trunk floras in mesic woods. Their occurrence high above the ground suggests humidity and

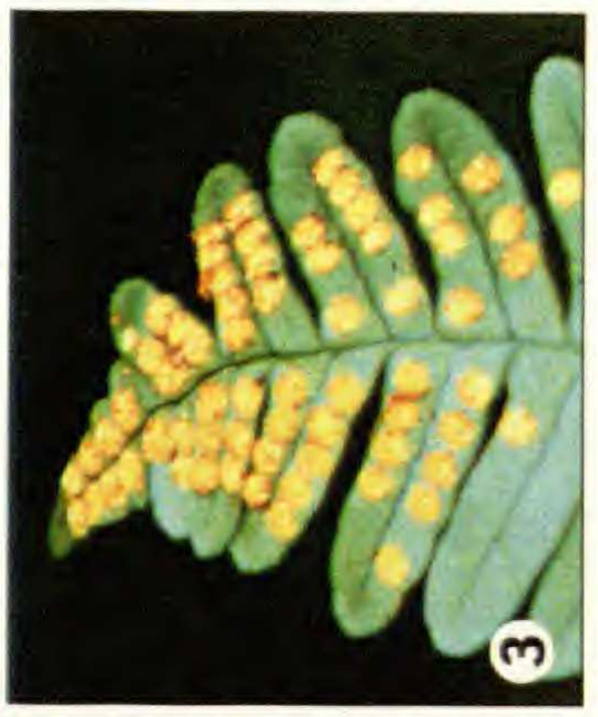

TABLE 1. Bryophytes identified from yellow poplar tree #307. Bark samples collected from various heights above ground as indicated. Liverwort names are indicated with *, moss names are unmarked.

Species	Height above ground (meters)						
	3.05	30.48	33.53	35.05	36.58	39.62	42.67
Anomodon attenuatus (Hedw.) Hueb.	×	×			×		
Brotherella tenuirostris (Bruch & Schimp.) Fl.	×						
Campylium chrysophyllum (Brid.) J. Lange	×						
Dicranum montanum Hedw.			×				
Dicranum viride (Sull. & Lesq.) Lindb.	×			×	×	×	
Fissidens subbasilaris Hedw.		×	×		×		
**Frullania sp.*	×				×	×	
**Frullania asagrayana* Mont.					×	×	
**Frullania brittoniae* Evans		×	×				
Haplohymenium triste (Ces. *ex* Denot.) Kindb.			×		×	×	×
**Harpalejeunea ovata* subsp. *integra* Schust.	×	×			×	×	
**Jamesoniella autumnalis* (DC.) Steph.					×		
**Lejeunea lamacerina* subsp. *gemminata* Schust.					×		
**Lejeunea ruthii* (Evans) Schust.	×				×	×	
**Lejeunea ulicina* (Tayl.) Gott.		×	×		×	×	
Leucodon brachypus Brid.		×	×		×	×	×
**Metzgeria sp.*			×		×	×	
Orthotrichum sp.			×				
Platygyrium repens (Brid.) BSG			×			×	
**Porella platyphylla* (L.) Pfeiff.			×				×
**Radula obconica* Sull.	×						
Rhodobryum roseum (Hedw.) Limpr.				×			
Thuidium delicatulum (Hedw.) BSG	×			×			
Trichostomum tenuirostre (Hook. & Tayl.) Lindb.					×		

light conditions similar to that found at tree bases. Bryophyte voucher specimens are deposited at the University of North Alabama (UNAF).

A horizontal branch at 35 m was the site of a microhabitat where mosses and ferns were confined to the upper surface, extending for about 4 m along the branch (Fig. 1). In order of their abundance, the mosses included *R. roseum*, (Fig. 2), *Thuidium delicatulum*, *Platygyrium repens*, and *Anomodon attenuatus*. These mosses provided a loose, soil-forming mat of humus approximately 10 to 14 cm thick that supported the creeping *P. appalachianum* rhizomes. *Polypodium appalachianum* was in several stages of development including infertile and fertile blades, the latter with immature, yellowish green sori and

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FIGS. 1–5. *Polypodium appalachianum* and *Rhodobryum roseum*. 1. Habit of epiphytic *P. appalachianum* collected from horizontal branch in the tree canopy; scale bar = 12 mm. 2. Habit view of *Rhodobryum roseum*., the bright green moss growing in dense patches of terminal rosettes, and other mosses forming a thick, humus mat; scale bar = 4.7 mm. 3. Fertile blade with immature sori on upper one-third of blade; scale bar = 6 mm. 4. Mature sori present on upper portion of blade; scale bar = 5 mm. 5. Mature rusty-red sori showing dehisced sporangia; scale bar = 6.5 mm.

mature, rusty red sori with, dehisced sporangia (Figs. 1, 3–5). *Polypodium appalachianum* was also observed growing on another horizontal branch at 40 m.

MORPHOLOGICAL DESCRIPTION OF TREE CANOPY POLYPODIUM APPALACHIANUM (FIGS. 1, 3–5).—Plants gregarious, creeping rhizomes embedded in moss and humus; leaves 5 to 16 cm long, blade deltate, 2.3 to 5.3 cm at widest point near the base; ultimate segments thin, flexible, linear to oblong with acute to narrowly rounded apices, broader at base, 0.4 to 0.8 cm wide, margins entire to crenulate, upper surface and midrib glabrous; venation free; sori on distal 1/3 to 1/2 of blade, borne abaxially at tips of single veins, lacking indusia, located midway between margin and midrib of the ultimate segments, 1.5 to 2.0 mm in diameter, circular when immature; sporangiasters more than 40 per sorus, heads densely covered with glandular hairs; spores ovate, with rough ornamentation of low, flattened projections, verrucose, 38 to 42 μm in length, falling within the diploid range. Voucher specimen deposited at the University of Kansas R. L. McGregor Herbarium (KANU).

DISCUSSION

Polypodium appalachianum was collected on August 2, 2001, falling within the summer and fall seasonal sporulation for this species. According to Haufler and Windham (1991), *P. appalachianum* is diploid with a chromosome number of 2n = 74, occurring from southeastern Canada, southward along the Appalachian Mountains and eastern seaboard states to Georgia and Alabama. Montgomery (1996) noted the habitat for *P. appalachianum* as mostly on rocks, boulders, ledges, cliffs, or rocky woods. A few specimens were recorded from tree trunks or bases of trees. Our collection is the first published record of *P. appalachianum* in the tree canopy. *Polypodium appalachianum* was previously treated as part of a single polymorphic taxon, *P. virginianum*, with 2n = 148, now understood to be an allotetraploid having *P. appalachianum* as one of its progenitor diploids (Haufler *et al.*, 1993).

What conditions have developed over time to provide a suitable habitat for *P. appalachianum* to become established, develop fertile sporophytes, and spread over several meters on just the upper surface of a horizontal branch? Barkman (1958) noted that *Polypodium* species produce a dense mat of roots with many fine hairs that serve to trap and retain moisture and nutrients. Thick horizontal branches provide a microhabitat that leads to heavy snow cover in winter protecting the epiphytes against frost and desiccation. In addition more dust, sand, and particulate matter accumulate over time to provide a thick humus greater than on the vertical trunk of the tree, thus favoring the establishment of terrestrial moss and fern species. Certainly the size of this tree would suggest a life span of more than 400 years. Litter and moss samples from the fern site were sent to Dr. Ernest C. Bernard at the University of Tennessee. His analysis of these samples for apterygotes indicated that the canopy collembola (springtails) fauna was distinct from that of the ground fauna, with little or no overlap in species composition. In addition to the collembola taxa

collected from this site, which will be published elsewhere, the discovery of *Acerentulus confinis* (Berlese), a proturan, was a puzzling find, because this group had been considered to be strict soil and litter organisms. The proturans have no known capacity for dispersing to the canopy of trees and surviving there.

The tree canopy of old growth forests in eastern United States remains largely unexplored for a myriad of different organisms. The discoveries documented here demonstrate that these habitats should not be taken for granted because they may yield insights on the origin of epiphytes. Whereas there is no doubt that special adaptations evolve in some epiphytic species (e.g., Benzing, 2000), our observations provide support for hypotheses that aerial habitats can mimic those on the forest floor (Bohlman et al., 1995) and provide opportunities for remarkable vertical disjunctions. Our results should encourage others to search in treetops to fully inventory and sample the biodiversity that exists in this aerial ecosystem.

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Literature Cited

Barkman, J. J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes including a Taxonomic Survey and Description of their Vegetation Units in Europe*. Koninklyke Van Forcum & Comp. N.V., Assen, Netherlands.

Benzing, D. H. 2000. *Bromeliaceae: Profile of an Adaptive Radiation*. Cambridge University Press, New York.

Bohlman, S., T. Matelson and N. Nadkarni. 1995. Moisture and temperature patterns of canopy humus and forest floor soils of a montane cloud forest, Costa Rica. Biotropica 27:13–19.

Counts, J., L. Henley, M. Skrabal and K. L. Snell. 2000. Tree Canopy Biodiversity in the Great Smoky Mountains National Park. Inoculum 51(6):1–5.

Crum, H. A. and L. E. Anderson. 1981. *Mosses of Eastern North America. Vol. 1*. Columbia University Press, New York.

Gove, D. 1994. Ramsay Cascades Trail. Pp. 474–477, in: D. DeFoe, B. Giddens, and S. Kemp (eds.). *Hiking Trails of the Smokies*. Great Smoky Mountains National History Association, Gatlinburg, Tennessee.

Haufler, C. H. and M. D. Windham. 1991. New species of North American *Cystopteris* and *Polypodium*, with comments on their reticulate relationships. Amer. Fern J. 81:7–23.

———, ———, F. A. Lang and S. A. Whitmore. 1993. *Polypodium*. Pp. 315–323, in *Flora of North America North of Mexico, vol. 2*. Flora of North America Editorial Committee. Oxford University Press, New York.

Montgomery, J. D. 1996. *Polypodium appalachianum*, *P. virginianum*, and their hybrid in New Jersey and Pennsylvania. Bartonia 59:113–117.

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and Allied Plants, with Special Reference to Tropical America*. Springer-Verlag, New York.